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Correlates of population genetic differentiation in marine and terrestrial environments

Lauren M. Schiebelhut  | Michael N Dawson 

School of Natural Sciences, University of
California, Merced, California

Correspondence

Lauren M. Schiebelhut, School of Natural
Sciences, University of California, Merced,
CA.

Email: lschiebelhut@gmail.com

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Abstract

Aim: Theory predicts that differences in phylogeographic structure between species should be related to differences in life history, environment, and evolutionary time. Reviews of empirical studies suggest sometimes complex interactions and possibly a preponderance of exceptions to the predicted relationship that greater population genetic differentiation results from lower dispersal potential, as a function of life history. We apply an analytical framework, which controls for effects of environment and time, to test the hypothesis that contrasts in population genetic differentiation are proportional to contrasts in life history traits.

Location: Global.

Methods: We conducted a meta-analysis using contrasts of life history traits and population genetic differentiation between synchronously diverging codistributed (SDC) taxa. Because SDC taxa experienced the same environment at the same time, the effects of time and environment are effectively controlled when analysing other causes of genetic differentiation within SDC taxa. This offers the opportunity to rigorously test whether traits favouring greater dispersal potential—such as fecundity, census population size, and duration of the dispersive stage—do lead to lower population genetic differentiation.

Results: We find a strong inverse relationship between dispersal potential and population genetic differentiation, consistent with predictions. SDC species pairs with similar dispersal potential show similar population genetic differentiation; species with higher dispersal potential have lower population genetic differentiation, relative to species with lower dispersal potential.

Main conclusions: SDC comparisons provide a rigorous method for disentangling the factors driving patterns of genetic differentiation in the marine and non-marine realms. We found broad support for the relationship that higher dispersal potential is associated with lower population genetic differentiation, the specifics of which can be influenced by place, time, and taxon. This relationship appears to be stronger on land than in the sea. However, many factors influence population genetic structure; deviations in measured versus predicted population genetic differentiation may indicate the influence of drift or selection. Too often, too many factors go unmeasured, constraining our ability to disaggregate dispersal syndromes and fully resolve the influence of specific life history characteristics on gene flow.

KEYWORDS

birds, community genetics, comparative phylogeography, dispersal syndrome, fishes, functional trait, gene flow, life history, marine invertebrates, synchronously diverging codistributed (SDC) species

1 | INTRODUCTION

Genetic variation is pervasive, yet distributed heterogeneously within and among species and geographically. Understanding how population genetic structure is shaped by the interplay between dispersal and selection remains one of the “Grand Challenges” in biology (Lindsay, 2012) despite decades of study. For example, long-standing theory predicts that phylogeographic structure should be shaped by life history, environment, and coalescent age (Marko & Hart, 2011), but reviews of empirical studies have suggested sometimes complex interactions (Bohonak, 1999) and possibly a preponderance of exceptions (Selkoe et al., 2010; Weersing & Toonen, 2009) to the intuitive generalization that increasing dispersal potential should lead to reduced population genetic differentiation (Stevens et al., 2013; Waples, 1987).

The lack of consensus may have several explanations. There could be epistemological problems: theory could be wrong or unrepresentative of natural situations, and expectations for simple relationships could be unrealistic. Alternatively, interpretation may be confounded by differences between taxa—for example, in life history, ecology, population size—as well as by differences in history that influence the contemporary distribution of genetic variation (Marko et al., 2010); moreover, complex traits or behaviour may alter how species interact with their environment (Costa, 1998; Shanks, 2009) in different circumstances and make it challenging to resolve the effect of a trait, such as pelagic duration (*PD*) in the marine realm, on population genetic differentiation. Additionally, emphases may have been on subsets of mechanisms rather than on their interplay and may have been studied to differing extents in different environments (Bohonak, 1999). For example, in the marine realm, migration has been credited as the main driver in structuring populations, although only recently have studies started paying equal attention to the influence of other mechanisms of evolution, particularly natural selection and genetic drift (Sanford & Kelly, 2011). In terrestrial systems, much attention has been focused on the influence of natural selection (e.g., Endler, 1986), but genetic drift and gene flow can still have a marked influence on the distribution of genetic variation among populations (Farkas, Hendry, Nosil, & Beckerman, 2015).

A fourth explanation for the lack of consensus may be that methods used to address this question have been insufficient. Identifying the causal relationships between traits, mechanisms of evolution, and phylogeographic patterns is difficult in natural systems, due to multiple complex levels of interlinked processes. Consequently, some studies may be suggestive but inconclusive. To reduce complexity and strengthen inference, simplified study systems that allow

for control or constraint of some variables have been sought out. One such approach is comparison of sister species (Hickerson et al., 2010; Lynch, 1989), but sympatric sister species are relatively rare in nature. An alternative approach, one that should be more abundant in nature, may be contrasts of life history traits and population genetic differentiation between taxa that are synchronously diverging and codistributed (SDC): taxa which have similar duration of evolutionary history and are distributed across a similar geographic area, that is, species which arguably have experienced similar environments for similar periods of time. These SDC species comparisons should, like sympatric sister species comparisons, control for effects of environment and time, offering the opportunity to test whether traits favouring greater dispersal (e.g., higher fecundity, larger population size, and differences in other dispersal-linked traits) lead to lower population genetic differentiation (Crisp, 1978; Dawson, 2014a; Doherty, Planes, & Mather, 1995; Gooch, 1975; Hellberg, 1996; Hoffman, Clarke, Linse, & Peck, 2010; Jablonski, 1986; Paulay & Meyer, 2006; Scheltema, 1971; Shanks, Grantham, & Carr, 2003; Trembl et al., 2012; Waples, 1987). Like sister species comparisons (Dawson, Louie, Barlow, Jacobs, & Swift, 2002), recent studies have found that SDC contrasts in population genetic differentiation can be explained largely by contrasts in fecundity (*F*), census population size (*N_c*)—both of which act to increase reproductive output and increase the chance and frequency of dispersal events (Trembl et al., 2012)—and other dispersal-linked traits (e.g., pelagic duration in marine taxa) or their co-correlates (Dawson, 2014a; Dawson, Hays, Grosberg, & Raimondi, 2014). In cases where empirical contrasts deviate from predicted contrasts, genetic drift and selection may be playing important roles in shaping population genetic structure.

Here, we explore the generality of the predicted relationship between dispersal and population genetic differentiation by conducting a meta-analysis of SDC taxa in marine and terrestrial/aquatic settings. We test the hypothesis that increased population genetic differentiation is negatively correlated with traits including fecundity (*F*), census population size (*N_c*), and others linked to dispersal (such as pelagic duration in the marine realm).

2 | MATERIALS AND METHODS

2.1 | The SDC approach

The basic building block of an SDC analysis is a time-calibrated contrast—of factors (e.g., traits that may influence drift, migration, selection) and response variables (e.g., estimates of population genetic differentiation such as F_{ST} , φ_{ST})—between a pair of taxa to quantify



effect sizes. The steps of an SDC analysis are to identify a suite of taxa that present a range of character states sufficient to test a chosen hypothesis, to estimate the duration of the evolutionary history that has contributed to the modern pattern of genetic diversity within each taxon, to gather distributional data describing the extent to which the taxa are codistributed, and, by contrasting only those taxon pairs that are SDC, to quantify differences in treatments and the corresponding effect size. The approach is described in detail by Dawson (2014a) and employed by Dawson et al. (2014). Here, we extend the SDC methodology to a meta-analytical framework, integrating the result of many such contrasts—that is, multiple estimates of effect sizes given multiple treatments of known magnitude—from a suite of global comparisons.

2.2 | The meta-analysis

We conducted a meta-analysis of data describing SDC pairs in the peer-reviewed published literature. We discovered articles by searching Web of Science (last search on 2 July 2018) using the following terms: “comparative phylogeograph*” plus (“co-distributed” or “codistributed” or “sympatr*”) plus (“time to most recent common ancestor” or “tMRCA” or “divergence time” or “coalescen*”). To broaden coverage of the literature, including identifying appropriate articles not recovered by the Web of Science search we also randomly searched approximately one-third of articles returned by Google Scholar using the same search terms except “coalescen*” (which yielded an unmanageable number of articles). The Web of Science search yielded zero marine SDC pairs, although we know from our own publications that some exist, so we also filtered the full Google Scholar results to extract all marine studies. Duplicates and non-peer-reviewed reports or conference abstracts that were misclassified as Journal Articles by Google Scholar were manually removed when compiling the final list of articles for analysis.

All articles included in the final analysis contained at least one pair of taxa that were (a) synchronously diverging, that is, the coalescent of each fell within the 95% credibility interval of the other (or, if only a range was provided, the median of the range fell within the range of the paired taxon), and (b) codistributed, that is, at least 70% of their ranges overlap as a rule of thumb (Dawson, 2012). Additionally, articles were included only if sufficient information was available to compare measures of population genetic structure and dispersal potential. The article itself had to contain (c) estimated F_{ST} , ϕ_{ST} , or analogous descriptors of population differentiation (either global or mean pairwise with 95% CI) using the same locus, and provide (d) information on fecundity (F), census population size (N_c), or other dispersal-linked traits, or such information had to be available or estimatable from other literature. In cases where three species met the SDC criteria in a single study, two of the three possible pairs were randomly selected to be included in the meta-analysis to avoid the statistical problem of nonindependence of comparisons.

We tested whether population genetic differentiation is influenced by traits including fecundity (F), census population size (N_c),

dispersal duration (e.g., pelagic duration in the marine realm [PD]), and/or co-correlates—that is, other life history, behavioural, physiological, or morphological traits contributing to “dispersal syndromes” (Clobert, le Galliard, Cote, Meylan, & Massot, 2009; Dawson, 2014b)—for all SDC pairs and then for terrestrial/freshwater and marine taxa separately. We used χ^2 tests against a null hypothesis of no relationship. Achieved power was calculated using G* POWER 3 (Faul, Erdfelder, Lang, & Buchner, 2007). Effect sizes were calculated for SDC pairs for which dispersal potential could be estimated quantitatively (Dawson et al., 2014).

Predicted contrasts in the number of migrants per generation (PN_m) were calculated from quantitative estimates of dispersal potential, when available, and compared to empirical contrasts, EN_m , inferred from measured F_{ST} for SDC taxa (see Dawson et al., 2014 for example of published implementation of this approach). We use Nm in our analysis because it is readily estimated from both dispersal potential and F_{ST} and acts as a common comparator (e.g., Dawson, 2014a, 2014b). However, we acknowledge that precise estimation of Nm from F_{ST} is difficult (Whitlock & McCauley, 1999), particularly in non-equilibrium species with high gene flow given a small error in F_{ST} may translate into a larger error in Nm (Waples, 1998) and may be correct only within a few orders of magnitude (Whitlock & McCauley, 1999). Fecundity (F) and census population size (N_c) were taken from the literature when available. When N_c was unavailable, study sample sizes were used as a proxy since we were primarily interested in relative abundances of the two species in the SDC pair, that is, we made the assumption that approximately equal effort was applied to collecting both species and took differences in sample sizes as indication of one species being generally more common than the other. F and N_c were used as direct proportional estimates of Nm , and PD was converted using the regression of Doherty et al. (1995) $\log F_{ST} = -0.043 (\text{no. of days}) - 0.315$ followed by $Nm = (1/F_{ST} - 1)/4$ following Dawson et al. (2014). Overall predicted Nm per species was calculated as the product of Nm taken from F , N_c , and PD , or whichever subset of information was available. The predicted contrast (PN_m) for pairs of SDC taxa was then calculated as a ratio of the higher dispersing species' $^PN_{m1}$ over the lower dispersing species' $^PN_{m2}$, and therefore always yields a contrast of ≥ 1 . Empirical contrasts (EN_m), from measured estimates of F_{ST} , also were calculated as a ratio of the species with higher predicted dispersal divided by the species with lower predicted dispersal. Here, values could be $^EN_{m1}/^EN_{m2} \geq 1$, indicating general support for the relationship between dispersal potential and gene flow, but values also could be ≤ 1 indicating a lack of support for the predicted relationship. The logarithm was then plotted for each of the two ratios. The theoretical expectation that contrasts in overall dispersal potential predict contrasts in empirically inferred Nm is represented by $^PN_{m1}/^PN_{m2} \approx ^EN_{m1}/^EN_{m2}$. Thus, we draw conclusions from two aspects of the Nm contrasts: (a) the quadrant to which the SDC pair plots and (b) the position of the pair within the positive quadrant—the upper left triangle ($^EN_m > ^PN_m$) or the lower right triangle ($^EN_m < ^PN_m$).

3 | RESULTS

The literature survey returned a total of 528 papers, 86 of which were from Web of Science and 442 from Google Scholar (Supporting Information Appendix S1). We read a total of 295 papers including all 86 from Web of Science, 159 (36%) selected randomly from Google Scholar, and all 50 remaining marine papers from the Google Scholar search. The survey yielded 23 papers containing 32 species pairs—14 marine and 18 terrestrial/freshwater—that met the criteria for SDC comparisons and had sufficient information available to make an estimate of dispersal potential (Table 1 and Table S1 in Supporting Information Appendix S2; data sources in Appendix 1). SDC-appropriate papers appeared more frequently in *Molecular Ecology* than any other journal. Many of the main animal phyla were represented, though vertebrates had greatest representation (Figure 1). Terrestrial pairs were distributed across five continents and marine pairs came from the Pacific Ocean and Indian Ocean (Figure 2).

Overall, SDC taxa with similar dispersal potential usually show similar population genetic differentiation (six of eight pairs), and those with higher dispersal potential usually have lower population genetic differentiation (19 of 24 pairs), consistent with predictions (Figure 3; Table 1). We found an inverse relationship between population genetic differentiation and F , N_c , and other dispersal-linked traits with the full dataset of SDC pairs ($n = 32$, $\alpha = 0.05$, $\chi^2 = 10.13$, $df = 1$, power = 0.89). The relationship between population genetic differentiation and dispersal potential is also supported in the terrestrial dataset alone ($n = 18$, $\alpha = 0.05$, $\chi^2 = 8.00$, $df = 1$, power = 0.81). However, although the majority (10 v. 4) of marine pairs support the prediction and the mean effect size is positive, the χ^2 -test lacks statistical power in the marine dataset alone ($n = 14$, $\alpha = 0.05$, $\chi^2 = 2.57$, $df = 1$, power = 0.36).

Quantitative descriptions of one or more dispersal-related traits existed for two-thirds of the SDC species pairs. In 10 cases, a single trait (F or PD) could be used to estimate predicted population genetic differentiation (Table 1), of which six cases showed that the species with higher PNm also had higher ENm and so reduced population genetic structure (Figure 4). However, it is the cumulative effect of multiple life history traits that should provide the best estimate of realized dispersal. Three additional cases allowed analysis of the combined effect of two traits (Table 1): comparison of New Zealand limpets (No. 3; Table 1), based on F and PD , contradicted the hypothesis that the contrast in PNm predicts the direction of the contrast in ENm ; comparison of skinks from the Ryukyu Archipelago of Japan (No. 32; Table 1), based on F and N_c , contradicted the hypothesis that the contrast in PNm predicts the direction of the contrast in ENm ; comparison of a barnacle and limpet in southeastern Australia (No. 1; Table 1), based on N_c and PD , supported the hypothesis that PNm_c predicts ENm_c . None of the SDC species pairs in our literature search had quantitative data for more than two dispersal-related traits.

When contrasts in the number of migrants per generation are compared per SDC pair, the contrast or effect size estimated as ENm_c is positively associated with the factor size (contrast in PNm_c)

in most cases (i.e., points occur in the positive quadrant in Figure 5), consistent with the hypothesis that inferred gene flow is generally a function of dispersal potential. The majority of terrestrial SDC species pairs fall in the upper left triangle of the positive quadrant (i.e., $ENm_c > PNm_c$) indicating that the estimated difference in dispersal potential explains only a portion of the measured difference in population genetic differentiation (Figure 5)—the farther the point is from the diagonal line (i.e., the greater the difference between the predicted and empirical ratios) the more influence that some other unmeasured factor has on population genetic differentiation. This same pattern is not seen in marine taxa, in which contrasts in PNm better correspond with contrasts in ENm (Figure 5). Of the six pairs of taxa that refute the relationship between dispersal potential and gene flow (Figure S2.1 in Supporting Information Appendix S2 identifies each point in Figure 5; Table 1), two showed no statistically significant difference when one was expected (No. 11 and 16; Table 1), three showed the species with higher dispersal potential had greater population genetic structure (No. 3, 29, and 32; Table 1), and one showed a slight difference when none was expected (No. 13; Table 1).

4 | DISCUSSION

As a general rule, we find population genetic structure is inversely related to dispersal potential. Species with higher dispersal potential—in terms of PD , F , N_c , a co-correlate, or “dispersal syndrome”—generally have lower population genetic differentiation than lower dispersal species, and species with similar dispersal potential generally have similar population genetic differentiation. For SDC species pairs with quantitative estimates of PD , F , or N_c , contrasts in PNm predict the direction of contrasts in ENm the large majority of the time (Figure 5). Deviations from the prediction may be a consequence of incomplete estimates of PNm or ENm —for example, data on life history and ecology generally were scarce, mathematical underpinnings are nonlinear—or suggest other mechanisms of evolution also play an interacting role in shaping population genetic structure. Below, we discuss select pairs of SDC taxa in more detail to explore the relationship between functional traits, dispersal potential, and population genetic structure as well as potential interactions with natural selection and genetic drift. Additionally, we highlight the need for more life history and ecological information as these are, more often than not, the limiting factors in analyses.

4.1 | Exceptions to “the rule”

Approximately eighty percent of SDC species pairs support the relationship between dispersal potential and gene flow based on the ecological data available in the literature. The twenty percent that are “exceptions to ‘the rule’” fall into two categories: (a) cases that probably can be explained with available data and (b) cases that cannot be explained with currently available data.

TABLE 1 Synchronously diverging codistributed (SDC) species by realm. The predicted relative F_{ST} (or analogue) is reported for each pair and is based on how known life history traits relate to dispersal potential; F_{ST} (or analogue) is reported and whether a positive relationship between dispersal potential and population genetic differentiation is supported. A list of the data sources is found in Appendix 1. Additional details for SDC pairs are in Table S1 in Supporting Information Appendix S2. Sample sizes and number of locations of samples are in Table S2 in Supporting Information Appendix S2

			Dispersal potential: population size (N_c), fecundity, and other dispersal related traits		Observed F_{ST} (or analogue)	
SDC pair	SDC reference (additional life history references)	SDC pairs		Predict F_{ST}^a		Result
Marine						
1	Ayre et al. (2009) (Stewart et al., 2007)	<i>Cellana tramoserica</i>	Broadcast spawn; relatively larger N_c ; pelagic duration 48 hr	Lower	0.335 ^b	Supports
		<i>Catomerus polymerus</i>	Eggs brooded; relatively smaller N_c ; pelagic duration 16 days	Higher	0.91 ^b	
2	Baums et al. (2014)	<i>Calcinus haigae</i>	Long pelagic duration; N_c not significantly different	Similar	0.004	Supports
		<i>Calcinus laevimanus</i>	Long pelagic duration; N_c not significantly different	Similar	0.006 ^b	
3	Goldstien (2005) (Goldstien et al., 2006; Dunmore & Schiel, 2000; Creese & Ballantine, 1983)	<i>Cellana ornata</i>	Pelagic duration 3–11 days; fecundity = 230,000	Lower	0.830 ^b	Refutes
		<i>Cellana radians</i>	Pelagic duration 3–11 days; fecundity = 105,000	Higher	0.142 ^b	
4	Hoareau et al. (2013)	<i>Ophiocoma brevipes</i>	Planktotrophic larvae	Similar	0.01847	Supports
		<i>Ophiocoma erinaceus</i>	Planktotrophic larvae	Similar	0.07006	
5	Hoareau et al. (2013)	<i>Ophiocoma cynthiae</i>	Planktotrophic larvae	Similar	0.14020 ^b	Supports
		<i>Ophiocoma scolopendrina</i>	Planktotrophic larvae	Similar	0.10851 ^b	
6	Hoareau et al. (2013)	<i>Ophiocoma erinaceus</i>	Planktotrophic larvae	Lower	0.07006	Supports
		<i>Ophioplocus imbricatus</i>	Lecithotrophic larvae	Higher	0.31463 ^b	
7	Hoareau et al. (2013)	<i>Ophiarachnella gorgonia</i> L1	Lecithotrophic larvae	Similar	−0.05653	Refutes
		<i>Ophiopeza fallax</i> L1	Lecithotrophic larvae	Similar	0.10647	
8	Marko et al. (2010)	<i>Katharina tunicata</i>	Planktonic larvae	Lower	−0.037	Supports
		<i>Xiphister atropurpureus</i>	Benthic larvae	Higher	0.296 ^b	
9	Ni et al. (2014)	<i>Larimichthys polyactis</i>	Pelagic duration 30 days	Lower	0	Supports
		<i>Octopus ocellatus</i>	Pelagic duration 0 days	Higher	0.87 ^b	
10	Ni et al. (2014)	<i>Pampus argenteus</i>	Pelagic duration 30 days	Lower	0	Supports
		<i>Octopus ocellatus</i>	Pelagic duration 0 days	Higher	0.87 ^b	
11	Ni et al. (2014)	<i>Rapana venosa</i>	Pelagic duration 21–42 days	Lower	0.01	Refutes
		<i>Engraulis japonicus</i>	Pelagic duration 14 days	Higher	0.02	
12	Plouviez et al. (2009)	<i>Bathymodiolus thermophilus</i>	Planktotrophic larvae; fecundity = 1,000,000	Lower	0.255 ^b	Supports
		<i>Eulepetopsis vitrea</i>	Lecithotrophic larvae; fecundity = 200	Higher	0.578 ^b	
13	Reece (2010) (Reece et al., 2011)	<i>Gymnothorax undulatus</i>	Pelagic duration 60–80 days	Similar	0.034 (95% CI 0.007–0.064)	Refutes
		<i>Echidna nebulosa</i>	Pelagic duration 60–80 days	Similar	0.002 (95% CI 0.000–0.007)	
14	Teske et al. (2011)	<i>Siphonaria concinna</i>	Planktonic disperser	Lower	0.07 (95% CI 0.03–0.10)	Supports
		<i>Siphonaria nigerrima</i>	Direct developer	Higher	0.30 (95% CI 0.22–0.39)	
Terrestrial						
15	Bagley and Johnson (2014) (Lucinda, 2003; Froese & Binohlan, 2000; Bussing, 1998; Baensch & Riehl, 1985)	<i>Alfaro cultratus</i>	Lifetime reproductive output 244–7,314; relatively larger N_c	Lower	0.73–0.80 ^b	Supports
		<i>Xenophallus umbratilis</i>	Lifetime reproductive output 224–748; relatively smaller N_c	Higher	0.99 ^b	

(Continues)

TABLE 1 (Continued)

SDC pair	SDC reference (additional life history references)	SDC pairs	Dispersal potential: population size (N_c), fecundity, and other dispersal related traits	Predict F_{ST}^a	Observed F_{ST} (or analogue)	Result
16	Carnaval et al. (2007) (Giaretta et al., 2008)	<i>Proceratophrys boiei</i>	Larval phase; fecundity = 1,296	Lower	0.72 (95% CI 0.60–0.85)	Refutes
		<i>Ischnocnema gr. ramagii</i>	Direct developing; fecundity = 21.5	Higher	0.8 (95% CI 0.69–0.91)	
17	Cook et al. (2014) (Juan-Jordá et al., 2013; Allen et al., 2002; Winemiller & Rose, 1992; Allen, 1989)	<i>Pseudomugil gertrudae</i>	Length 3.8 cm (size \propto fecundity)	Similar	0.815 ^b	Supports
		<i>Denariusa australis</i>	Length 4.5 cm, commonly 3.5 cm (size \propto fecundity)	Similar	0.826 ^b	
18	Guzik et al. (2009)	<i>Paroster microsturtensis</i>	Relatively larger N_c ; body size 1.8 mm (favourable for dispersal given environment)	Lower	0.01	Supports
		<i>Paroster macrosturtensis</i>	Relatively smaller N_c ; body size 4 mm (less favourable for dispersal given environment)	Higher	0.6 ^b	
19	Hosner et al. (2014) (Fishpool & Tobias, 2016; Cheke et al., 2001)	<i>Prionochilus olivaceus</i>	Fecundity = 1–4	Similar	0.92 ^b	Supports
		<i>Pycnonotus urostictus</i>	Fecundity = 3	Similar	0.90 ^b	
20	Kirchman and Franklin (2007) (Speakman, 2005)	<i>Chalcophaps indica</i>	Lifetime reproductive output 36–176	Lower	–0.025 ^c (pairwise range –0.096 to 0.042)	Supports
		<i>Rhipidura spilodera</i>	Lifetime reproductive output 15–31	Higher	0.336 ^c (pairwise range 0.181 to 0.545)	
21	Kirchman and Franklin (2007) (Taylor, 2010; Speakman, 2005)	<i>Gallirallus philippensis</i>	Lifetime reproductive output 104–574	Lower	0.026 ^c (pairwise range –0.087 to 0.046)	Supports
		<i>Rhipidura spilodera</i>	Lifetime reproductive output 14–29	Higher	0.336 ^c (pairwise range 0.181 to 0.545)	
22	Kuo et al. (2014)	<i>Murina gracilis</i>	Extreme site fidelity and limited natal dispersal	Similar	0.05 ^b	Supports
		<i>Murina recondita</i>	Extreme site fidelity and limited natal dispersal	Similar	0.06 ^b	
23	Qu and Lei (2009)	<i>Onychostruthus taczanowskii</i>	Strong flight ability and a tendency to seasonal altitudinal movements	Lower	0.02725	Supports
		<i>Pseudopodoces humilis</i>	Very active on the ground, but flies only rarely and weakly	Higher	0.21938 ^b	
24	Qu et al. (2010)	<i>Pyrgilauda blanfordi</i>	Strong flight and a tendency to altitudinal migration	Lower	0.0314	Supports
		<i>Eremophila alpestris</i>	Habitat specific and have restricted dispersal ability	Higher	0.1133 ^b	
25	Qu et al. (2010)	<i>Pyrgilauda blanfordi</i>	Strong flight and a tendency to altitudinal migration	Lower	0.0314	Supports
		<i>Montifringilla adamsi</i>	Habitat specific and have restricted dispersal ability	Higher	0.1302 ^b	
26	Schoville et al. (2012) (Honěk 1993)	<i>Nebria ingens</i>	Length 12–15 mm (size \propto fecundity)	Lower	0.676 ^b	Supports
		<i>Nebria ovipennis</i>	Length 9.5–12 mm (size \propto fecundity)	Higher	0.811 ^b	
27	Schoville et al. (2012) (Honěk, 1993)	<i>Nebria ingens</i>	Length 12–15 mm (size \propto fecundity)	Lower	0.676 ^b	Supports
		<i>Nebria spatulata</i>	Length 9.5–12 mm (size \propto fecundity)	Higher	0.788 ^b	

(Continues)

TABLE 1 (Continued)

SDC pair	SDC reference (additional life history references)	SDC pairs	Dispersal potential: population size (N_c), fecundity, and other dispersal related traits	Predict F_{ST}^a	Observed F_{ST} (or analogue)	Result
28	Whiteman et al. (2007)	<i>Colpocephalum turbinatum</i>	Moderate relative dispersal ability (horizontal transmission); mean abundance 74.59 (58–89.98)	Lower	0.73 ^b	Supports
		<i>Degeeriella regalis</i>	Low relative dispersal ability (vertical transmission during brooding); mean abundance 14.36 (11.05–17.51)	Higher	0.85 ^b	
29	Whiteman et al. (2007)	<i>Icosta nigra</i>	High relative dispersal ability (volant and vagile); mean abundance 1.49; lower fecundity	Higher	0.63 ^b	Refutes
		<i>Colpocephalum turbinatum</i>	Moderate relative dispersal ability (horizontal transmission); mean abundance 74.59 (58–89.98); higher fecundity	Lower	0.73 ^b	
30	Zhang et al. (2013)	<i>Fagus lucida</i>	Similar life history; relatively larger N_c	Lower	0.705 ± 0.067	Supports
		<i>Fagus longipetiolata</i>	Similar life history; relatively smaller N_c	Higher	0.936 ± 0.036	
31	Dellicour et al. (2015)	<i>Melitta nigricans</i>	Similar life history; relatively larger N_c	Lower	0.776 ^c	Supports
		<i>Melitta tricincta</i>	Similar life history; relatively smaller N_c	Higher	0.875 ^c	
32	Kurita and Toda (2017) (Brandley et al. 2011; Novosolov & Meiri, 2013)	<i>Plestiodon stimpsonii</i>	Clutch size 9; $N_c = 5 \times N$. <i>kishinouyei</i> ; dense forest habitat	Lower	0.34 ^b	Refutes
		<i>Plestiodon kishinouyei</i>	Clutch size 3; $N_c = 1/5 P$. <i>stimpsonii</i> ; open environment habitat	Higher	0.19 ^b	

Notes. Four additional SDC pairs were excluded from the meta-analysis for lack of independence (i.e., when three species were SDC, one of the three possible pairs were randomly selected for exclusion). Had these additional pairs—*Ophiocoma brevipes* and *Ophioplocus imbricatus* (O.b.–O.i.) (Hoareau et al., 2013); *Nebria ovipennis* and *Nebria spatulata* (N.o.–N.s.) (Schoville et al., 2012); *Chalcophaps indica* and *Gallirallus philippensis* (C.i.–G.p.) (Kirchman & Franklin, 2007); *Degeeriella regalis* and *Icosta nigra* (D.r.–I.n.) (Whiteman et al., 2007)—been included, three would support (O.b.–O.i., N.o.–N.p., C.i.–G.p.) and one would refute (D.r.–I.n.) the relationship between dispersal potential and gene flow.

^a F_{ST} is used as shorthand to represent other measures of population genetic differentiation.

^bGenetic differentiation significant at least at $p < 0.05$.

^cSignificance not reported.

In the first category, of the seven pairs reported as “refuting” the pattern, three were from islands (No. 3, 29, and 32, Table 1 and Table S1 in Supporting Information Appendix S2). In island situations, genetic drift and selection are known to be important drivers of patterns of genetic variation (Losos & Ricklefs, 2009) and may overwhelm dispersal which is expected to be sporadic. Concomitantly, in both island studies, the predicted difference in dispersal did not manifest in empirical estimates of population genetic differentiation; rather, the species with higher P_{Nm} had lower F_{Nm} . Moreover, quantitative differences in F and N_c of bird lice (No. 29, Table 1) may be overcome by traits reported qualitatively: *Icosta nigra* is volant and vagile and so may have higher relative dispersal ability than *Colpocephalum turbinatum* which is transmitted via body to body contact between hosts (Whiteman, Kimball, & Parker, 2007).

In the second category are the remaining four of the seven SDC pairs reported as refuting the pattern. Two pairs—of brittlestars

(*Ophiarachnella gorgonia* L1 and *Ophiopeza fallax* L1; No. 7, Table 1) and eels (*Gymnothorax undulatus* and *Echidna nebulosa*; No. 13, Table 1)—were predicted to have no difference in P_{Nm} ; however, F_{ST} was -0.057 versus 0.106 for the brittlestars and 0.034 (95% CI 0.007 – 0.064) versus 0.002 (95% CI 0.000 – 0.007) for the eels, which translates into large differences in F_{Nm} . Two other pairs of ecologically disparate taxa—a marine snail versus fish (*Rapana venosa* and *Engraulis japonicus*; No. 11, Table 1) and a frog versus lizard (*Proceratophrys boiei* and *Ischnocnema gr. ramagii*; No. 16, Table 1)—were predicted to differ significantly, but no clear distinction was observed in F_{Nm} . But, in all four cases, life history data were limited (Table 1) and it is conceivable that variation in other traits likely are contributing to the observed differences. For example, the two eels’ PDs are similar (60–80 days; Reece, 2010) and, while the measured F_{ST} appears to refute ‘the rule’ (mean [95% CI]: 0.034 [0.007 – 0.064] vs. 0.002 [0.000 – 0.007]), both are clearly high dispersal species in

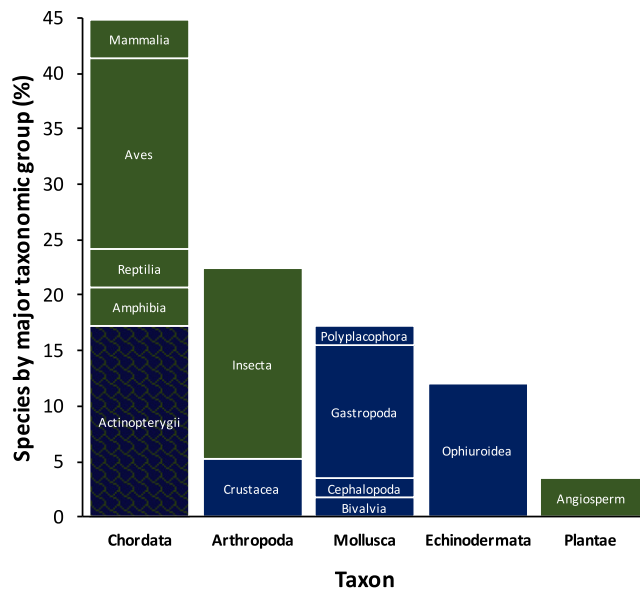


FIGURE 1 Summary of literature survey results satisfying synchronously diverging and codistributed (SDC) criteria (Table 1 and Table S1 in Supporting Information Appendix S2) showing the proportion of species representing major taxonomic groups by realm (blue = marine, green = terrestrial or freshwater).

theory and in reality; modest differences in F , N_c , or other traits, such as larval behaviour, could account for the modest differences observed in F_{ST} (Figure 3). Additionally, precise estimation of N_m from F_{ST} is difficult in species with high gene flow given (in addition to concerns about non-equilibrium) the inverse relationship between

F_{ST} and N_m (Waples, 1998). Likewise, the prediction for *R. venosa* and *E. japonicus* based on PD might be changed by a modest difference in other life history traits, as seen in Ayre, Minchinton, and Perrin (2009) (No. 1, Table 1).

Of course, one might argue that cases which currently support the hypothesized “rule” based on a single trait might change to refute the hypothesis when based on additional traits. This is a possibility; however, notwithstanding the “file drawer problem” of publication bias (Rosenthal, 1979), our approach to the literature survey should have yielded representative studies. We consider it unlikely that there is a sufficiently large systematic bias in our dataset that it would reverse the majority support for the hypothesis that increasing dispersal potential leads to reduced population genetic differentiation.

4.2 | Contrasts between regions within realms

A proposed advantage of meta-analyses of SDC pairs is the ability to explore both general trends, such as the relationship between dispersal potential and population genetic differentiation, and how such generalities are modified by interactions specific to locations or taxa (Dawson, 2014a). While the current dearth of life history data for most species limits the scope of current analyses, two examples enable us to briefly and cautiously explore the utility of contrasts between regions within realms. These examples build on the idea that habitat discontinuity is expected to reduce gene flow (Riginos & Nachman, 2001), in which case—all other things being equal—we might expect to see a smaller effect size of dispersal potential ($^P N_m$) on inferred gene flow ($^E N_m$) due to a stronger effect of selection and/or drift.

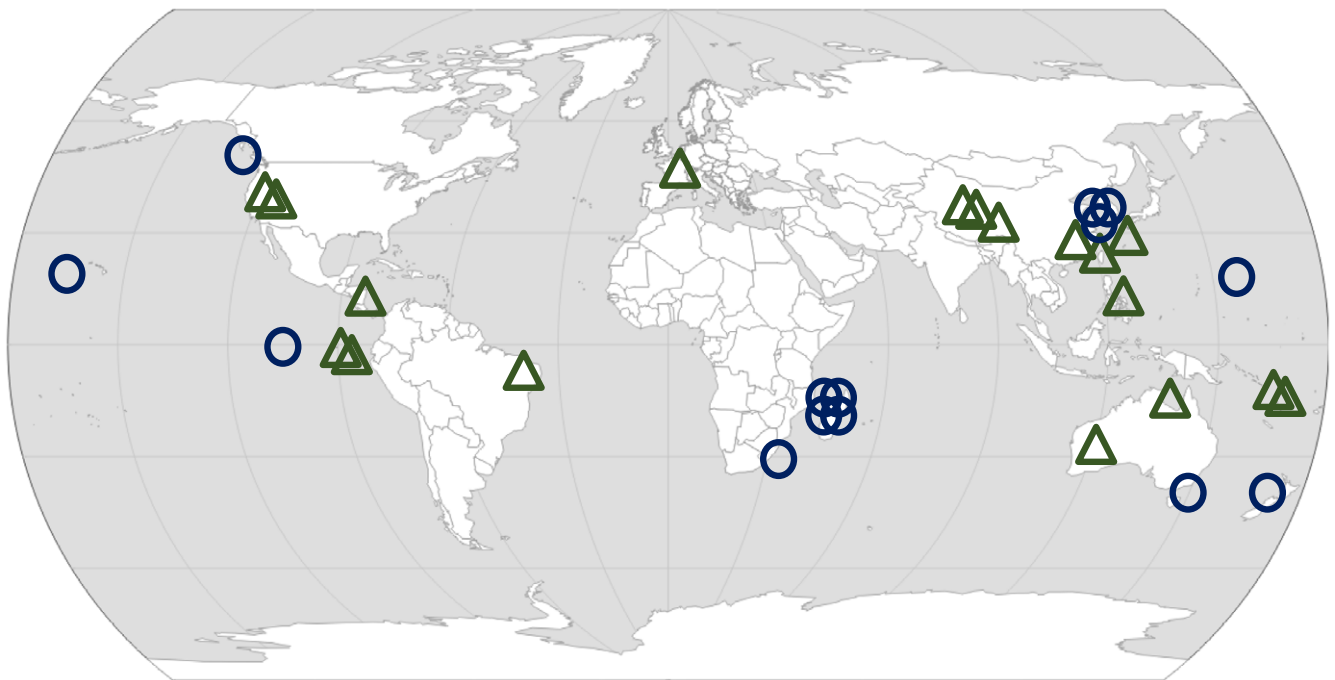


FIGURE 2 Geographic locations of synchronously diverging and codistributed (SDC) species pairs used in this study (Table 1 and Table S1 in Supporting Information Appendix S2). Blue circles correspond to marine pairs and green triangles correspond to terrestrial or freshwater pairs.

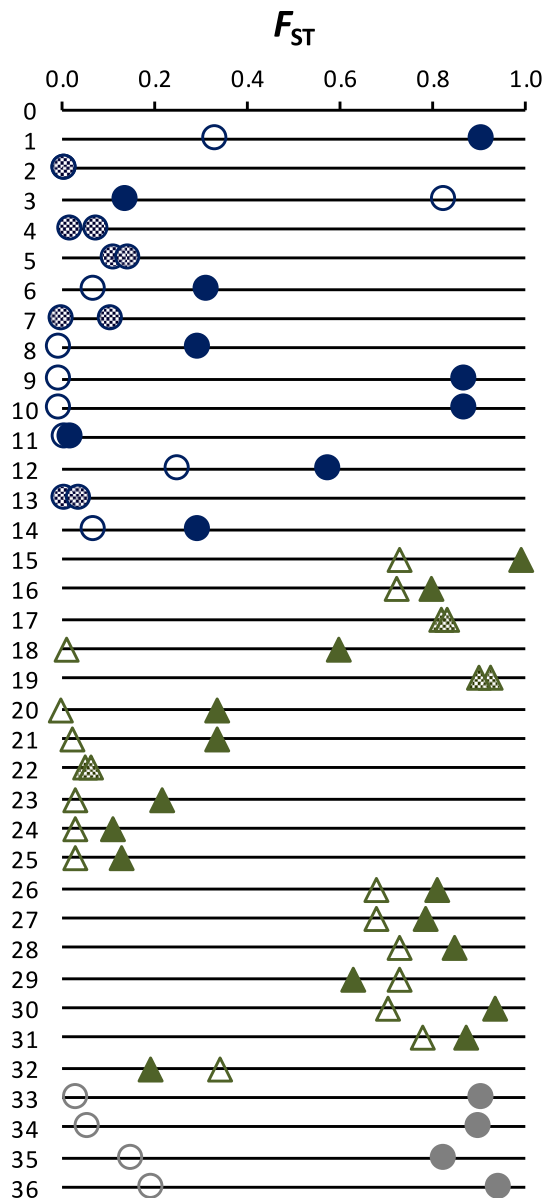


FIGURE 3 F_{ST} values for each synchronously diverging and codistributed (SDC) species pair (circles = marine, triangles = terrestrial/freshwater). Numbers 1–32 correspond to SDC pairs described in Table 1 and Table S1 in Supporting Information Appendix S2. Numbers 33–36 (grey) correspond to additional SDC pairs from Dawson et al. (2002, 2014) included for subsequent comparison. Open shapes represent the taxon in each SDC pair with higher predicted dispersal based on life history traits (and expected to correspond to lower F_{ST}); solid shapes correspond to the taxon with lower predicted dispersal (and expected higher F_{ST}). An open shape to the left of a closed shape indicates support for the hypothesis that the species with higher predicted dispersal has less genetic differentiation among populations. Patterned shapes represent pairs of taxa that are expected to have the same dispersal potential (and F_{ST}); when these patterned symbols are superimposed, they are consistent with the null hypothesis.

Contrasting two pairs of marine SDC taxa—whose PNm_c is within an order of magnitude but one occupying coastal regions, one occupying hydrothermal vent regions—we find PNm_c accounts for ENm_c in the pair with greater habitat connectivity, whereas PNm_c overestimates ENm_c in the pair with limited habitat connectivity. The first pair, a snail and limpet (*Nucella emarginata*–*Lottia austrodigitalis*, Dawson et al., 2014), occupies relatively continuous intertidal habitat along the west coast of the USA (Table 1 in Dawson et al., 2014), while the other pair, a mussel and limpet (*Bathymodiolus thermophilus* and *Eulepetopsis vitrea*, No. 12, Table 1), occupies patchily distributed deep-sea hydrothermal vents (Tunncliffe, McArthur, & McHugh, 1998; Vrijenhoek, 2009). For the coastal pair, the ratio of empirical Nm falls within the range of predicted Nm (range of $PNm_c = 16.8$ –3440 [median 1,728], $ENm_c = 144$; $PNm_c \approx ENm_c$), whereas for the hydrothermal vent pair, the ratio of empirical Nm is three orders of magnitude less than predicted Nm ($PNm_c = 5,000$, $ENm_c = 4$; $PNm_c \gg ENm_c$), suggesting the lack of habitat continuity influences the interaction between dispersal potential and gene flow. Despite a large difference in fecundity for the vent SDC pair (Table 1), patchiness in vent versus coastal habitats may contribute to dispersal dynamics and influence the realized rate of migration (Cowen & Sponaugle, 2009).

Similar to the marine example, we compare two pairs of terrestrial SDC beetles—one occupying the Sierra Nevada mountains and the other occupying subterranean aquifers—that appear to have similar PNm_c but differ in their degree of habitat continuity, and find that ENm_c deviates more from PNm_c for the pair associated with habitat that is more discontinuous. The first pair (*Nebria ingens*–*Nebria spatulata*, No. 27, Table 1) occupy habitat that is more continuous in the Sierra Nevada mountains in the USA, relative to the second pair (*Paroster microsturtensis*–*Paroster macrosturtensis*, No. 18, Table 1) that occupy aquifers described as “islands under the desert” (Cooper, Hinze, Leys, Watts, & Humphreys, 2002) in central Western Australia. For the Sierra Nevada pair, the ratio of empirical Nm is very similar to predicted Nm ($PNm_c = 1.3$, $ENm_c = 1.8$; $PNm_c \approx ENm_c$), whereas for the desert aquifer pair, the ratio of empirical Nm is two orders of magnitude greater than predicted Nm ($PNm_c = 1.3$, $ENm_c = 149$; $PNm_c \ll ENm_c$), suggesting the difference in environment or life history–environment interactions may contribute to the difference in observed gene flow.

For these two SDC examples, we see markedly different responses to what appears to be a similar difference in habitat connectivity. The taxon pairs occupying relatively continuous habitats meet the expectation of $PNm_c \approx ENm_c$, whereas the two pairs occupying relatively discontinuous habitats deviate from this expectation, but in different ways. Although we do not have the sample sizes to adequately explore this relationship, it seems likely SDC meta-analyses should be able to pull out important regional signals, but more and better quality data are needed for discerning subtle differences.

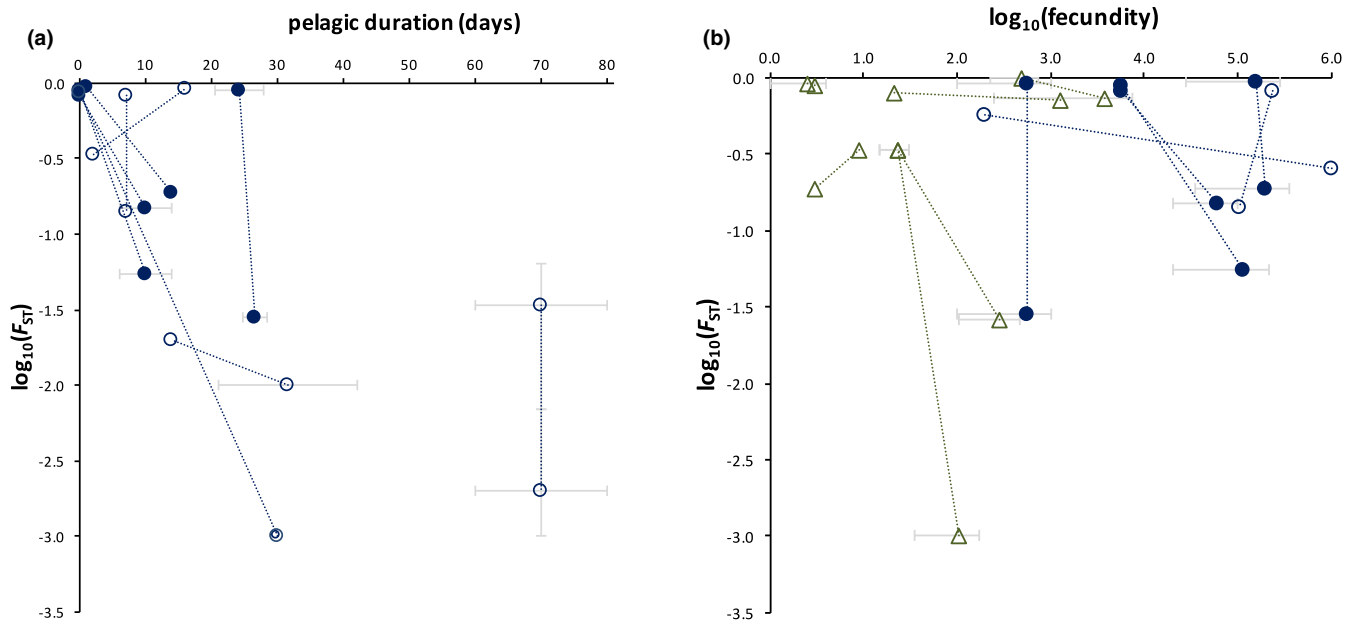


FIGURE 4 The relationship between select life history traits—(a) pelagic duration, PD , and (b) fecundity, F —and population genetic structure, F_{ST} , for synchronously diverging and codistributed (SDC) species pairs from this meta-analysis (open symbols) and for four additional SDC pairs from Dawson (2012) and Dawson et al. (2014) (closed symbols). SDC pairs used in (a) include 6, 7, 9–12 and (b) 5, 9, 15, 16, 19, 20, 23, 32 (Table 1 and Table S1 in Supporting Information Appendix S2). For fecundity, lifetime reproductive output is used when available, otherwise annual fecundity is reported; the metric used is consistent within SDC pairs. Each pair of points connected by a dotted line represents an SDC pair (marine = blue circles; terrestrial = green triangles). A negative slope indicates that differences in life history traits between SDC species contribute to a difference in genetic differentiation. Horizontal error bars represent the range of recorded values for pelagic duration or fecundity for each species and vertical error bars are 95% confidence intervals for F_{ST} , if this information was available.

4.3 | Contrasts between marine and terrestrial SDC taxa

Among the longest standing contrasts amongst regions of the world are those made between marine and nonmarine systems (Mayr, 1954; Paulay & Meyer, 2002; Smetacek & Pollehne, 1986; Steele, 1985; Vega & Wiens, 2012; Vermeij & Grosberg, 2010). Particularly, dispersal and gene flow are generally thought to be pervasively higher in marine versus terrestrial systems (e.g., Carr et al., 2003; Neigel, 1997). We find the majority of terrestrial species have $^E Nm_c > ^P Nm_c$ (i.e., in the upper left triangle of positive quadrant, Figure 5) whereas marine species tend to have $^E Nm_c \leq ^P Nm_c$ (lower right triangle, Figure 5), suggesting that SDC contrasts provide a mechanism for exploring factors influencing genetic diversity in terrestrial and marine environments. Consistent with the idea that there are statistical but not fundamental differences between the two realms—for example, density and viscosity of the water/air medium (Dawson & Hamner, 2008).

Terrestrial SDC species pairs had Nm ratios that suggest differences in empirically estimated Nm exceed differences predicted by dispersal potential alone (Figure 5). Such mismatch suggests selection and/or drift may be important (Grosberg & Cunningham, 2001) and thus may variously accentuate or diminish contrasts. Considering the effect of geographically varying selection, species with higher population genetic differentiation should exhibit more local adaptation

than those with elevated gene flow (Holt & Gaines, 1992). Indeed, isolation by environment is common in terrestrial taxa, whereas unrestricted gene flow is nearly twice as common in the marine realm (Sexton, Hangartner, & Hoffman, 2014). Thus, reduced gene flow may tend to allow disproportionately greater local adaptation in the lower dispersal species of an SDC pair and thus accentuate the contrast in observed $^E Nm_c$.

Exceptions to the general rule that “population genetic differentiation is inversely proportional to dispersal potential” may be reasonably common (~20%) and offer opportunities to better understand patterns of population genetic structure—if studied in an appropriate framework. The previously discussed mountain versus aquifer and coastal versus vent examples suggest that the SDC framework could provide the context to rigorously test the relative influence of habitat continuity and whether discontinuity acts to amplify (or diminish) differences in $^E Nm_c$ in the terrestrial (or marine) realm relative to that predicted by $^P Nm_c$.

4.4 | Considerations for future studies

Using the SDC framework to test hypotheses relating life history traits that influence dispersal potential to population genetic differentiation minimizes confounding factors that otherwise cloud inference (e.g., demonstrated in Figure S2.2 in Supporting Information Appendix S2) (Dawson, 2014a). The origins of the approach are

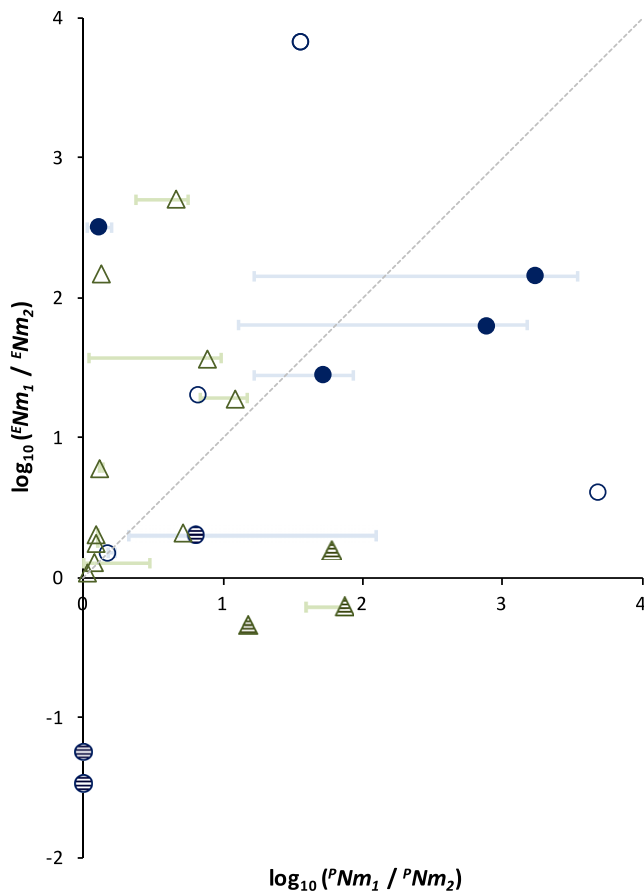


FIGURE 5 Comparison of the relative estimated numbers of migrants per generation (Nm) predicted from dispersal potential (x-axis) and inferred empirically from F_{ST} or an F_{ST} -analogue (y-axis) for pairs of synchronously diverging and codistributed (SDC) species. Blue circle = marine; green triangle = terrestrial/freshwater. Stripping indicates SDC pairs classified as refuting the predicted relationship (Table 1 and Table S1 in Supporting Information Appendix S2). In most cases, only a single trait could be assessed, except for three pairs for which two traits could be assessed. Points in the positive quadrant indicate a positive relationship between contrasts in dispersal potential and contrasts in population genetic structure and the closer a point is to the dashed grey line—which represents the relationship $PNm_1/PNm_2 \approx ENm_1/ENm_2$ —the more closely that SDC pair matches the theoretical expectation that differences in dispersal potential lead to corresponding differences in population genetic structure. The four solid-filled marine points represent SDC species contrasts from Dawson et al. (2002) (using F and PD ; Spies & Steele, 2016) and Dawson et al. (2014) (using F , N_c , and PD) to calculate Nm contrasts. Figure S2.1 provides a key to identifying which datapoints correspond with each SDC pair shown in Figure 3 and Table 1 and Table S1 in Supporting Information Appendix S2.

rooted in sympatric sister species comparisons (Dawson, 2012; Dawson et al., 2002; Hickerson et al., 2010) and expanded to include species that are, like sister species, synchronously diverging (Dawson, 2014a; Dawson et al., 2014). However, SDC analyses still can be improved in several ways: by incorporating species distribution models (SDMs), ecological niche models and palaeodistributions, exploring the mathematical nonlinearities associated with dispersal

potential and empirical estimates of gene flow, including additional molecular markers—although mtDNA provides a good first approximation (Bowen et al., 2014)—and by collecting more and better quality ecological data.

On the first count, integrating SDMs, ecological niche models, and palaeodistributions allows one to independently corroborate (or refute) modern distributional, and historical demographic, inferences about the degree of codistribution between species in the past and present (Dawson, 2014a). Better quantifying the duration of codistribution is important because species' histories can shape current distributions of genetic variation and can be complex (Knowles, 2009). Few of the studies reviewed here incorporated such analyses (but see Dellicour, Michez, Rasplus, & Mardulyn, 2015; Kuo, Chen, Fang, Flanders, & Rossiter, 2014; Schoville, Roderick, & Kavanaugh, 2012), and although such studies are rapidly increasing in number (Gavin et al., 2014), they remain much underemployed (Riddle, 2016).

Second, while a generally desirable property of Nm contrasts is that they reflect the *relative* magnitudes of differences in predicted and observed migration, different combinations of predicted and empirical Nm can lead to similar ratios of ENm_c and PNm_c . Moreover, the relationship between life history traits and population genetic structure may be nonlinear and potentially influenced by standing genetic diversity. Interpreting SDC contrasts therefore can be challenging if appropriate contextual information is lacking. The conceptual appeal of contrasting sympatric synchronously diverging taxon pairs within a multiple regression framework to estimate causes and effects (Hickerson et al., 2010) may mask multiple analytical complexities that likely require formulation and evaluation of multiple competing models (Hickerson et al., 2010). Nonetheless, our initial comparison provides a useful starting place to explore additional questions. For example, we do find terrestrial SDC taxa exhibit $ENm_c > PNm_c$ more often than marine SDC taxa; what (if anything) is the biological significance? Potential explanations could include the idea that population sizes, and so standing genetic diversity, are typically lower, that environmental resistance is typically greater, or that drift or selection is stronger in terrestrial than in marine systems (Carr et al., 2003).

Finally, and perhaps most importantly, more and better trait data are required, including behaviour. Only a single trait could be estimated in many of the cases we considered here (Table 1), whereas it is the cumulative influence of multiple traits that determine dispersal ability (Clobert et al., 2009; Dawson, 2014b; Dawson et al., 2014). For SDC pairs for which at least three traits were quantitatively assessed, Nm contrasts between dispersal potential and F_{ST} may adequately account for the relative magnitudes of differences in observed gene flow (Dawson et al., 2014). With multitrait data in hand, we might better understand how functional traits interact in dispersal syndromes and identify emergent properties of complex traits such as dispersal potential. However, comparison between realms will remain difficult as long as marine studies are underrepresented in the literature (Dawson et al., 2013; Whittaker, 2014). In our opinion, the major roadblock for understanding dispersal and population genetic structure is no longer the cost or logistics of large-scale genetic analyses,

nor available methods, the epistemological framework, nor theory, but rather a dearth of high quality comprehensive ecological data across multiple species, habitats, and realms.

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ORCID

Lauren M. Schiebelhut  <http://orcid.org/0000-0002-5417-5426>

Michael N Dawson  <http://orcid.org/0000-0001-7927-8395>

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BIOSKETCHES

Lauren Schiebelhut studies how life history, dispersal, and selection contribute to the distribution of spatial and temporal patterns of genetic variation, and how disturbance events (e.g., disease outbreaks, extreme environmental perturbation) can inform our understanding of the interacting roles they play in sculpting patterns of genetic diversity. She is particularly interested in using multiyear ecological and genetic monitoring to capture species' short-term evolutionary responses to ecological and environmental change.

Michael Dawson researches the geographic and temporal distributions of biodiversity from the perspectives of population genetics, genomics, systematics, and population and community ecology. This study complements collaborative projects in the north-eastern and western Pacific Ocean that seek to integrate environmental, ecological, and evolutionary processes.

Author contributions: M.N.D. conceived of the study, L.M.S. and M.N.D. conducted the literature search and screened papers, L.M.S. compiled data and performed the meta-analysis. L.M.S. wrote the first draft of the manuscript, and both authors contributed to revisions.

APPENDIX 1

DATA SOURCES

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SUPPORTING INFORMATION

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